prove of considerable value in bacteriological investigations. Further experiments are now being made with other organisms which up to the present time have not been proved to be absolutely distinct.

Numerous experiments were made on the resistance of these endotoxins to heat, and every result shows that they are thermostable even when exposed to a temperature of 100° C. for 30 minutes, and are still able to exert their specific action, as is shown by the following experiment:—

	No. of bacilli in 50 cells.	No. of non-phagocytic cells.
A. Serum saline + leucocytes + *B. coli*	233	0
B. Serum Danysz extract + leucocytes + *B. coli*	59	15
C. Serum coli extract + leucocytes + *B. coli*	4	46
D. Serum Danysz extract* + leucocytes + *B. coli*	59	16
E. Serum coli extract* + leucocytes + *B. coli*	6	44

* This extract was exposed to a temperature of 100° C. for 30 minutes.

On the Determination of the Chief Correlations between Collaterals in the Case of a Simple Mendelian Population Mating at Random.

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(1) In a paper communicated to the Royal Society in April, 1909, Prof. Pearson obtained the gametic correlations between the offspring and the ancestry in each grade in a simple Mendelian population mating at random. By a "simple Mendelian population" for a given character, he understood one which started with any definite ratio of dominant individuals (AA) to recedents (*aa*). These mating at random give rise to a population which may be written in the form

$$p^2\,(\mathrm{AA}) + 2pq\,(\mathrm{A}a) + q^2\,(aa),$$

and of which, without selection, the proportions of dominants, recedents, and hybrids are known to remain constant, with continued random mating, during successive generations. Prof. Pearson found that, both in the case of gametic and somatic characters, the ancestral correlations diminished in

a geometrical progression, and thus obeyed the fundamental principle of the Law of Ancestral Heredity, as deduced from observations on man and other living forms.

(2) It is difficult to believe that the characters dealt with in the case of Mendelian investigations on animals can be largely affected by environment, but it is easy to allow for this influence by the method of partial correlation. If, in an investigation on any given character, the subscript 1 denote offspring, 2 the ancestor in any generation, 3 the offspring's environment, and 4 the ancestor's environment, then the correlation between 1 and 2 for constant 3 and 4 is given by

$$ {}_{34}\rho_{12} = \frac{r_{12}(1-r_{34}^2) - r_{13}r_{23} - r_{14}r_{24} + r_{34}(r_{14}r_{23} + r_{13}r_{24})}{\{1 - r_{23}^2 - r_{34}^2 - r_{24}^2 + 2r_{23}r_{34}r_{24}\}^{\frac{1}{2}}\{1 - r_{13}^2 - r_{14}^2 - r_{34}^2 + 2r_{13}r_{34}r_{14}\}^{\frac{1}{2}}}. $$

If we suppose the environment of a given stock to remain constant, this reduces to the simple form

$$ {}_{e}\rho_{12} = \frac{r_{12} - e^2}{1 - e^2}, $$

where e is the correlation between character and environment.* This should be absolutely true for pairs of brothers reared in the same home conditions.

Many investigations into the value of e for a great variety of characters in man have been carried out in the Statistical Laboratory at University College, and these show that the value of e is remarkably small. Its average value is 0·03, and it rarely reaches an intensity as high as 0·1. It can only introduce a second order correction into the correlation, and one well within the limits of the probable error of the determination. If e were 0·1, the change in fraternal correlation would only be from 0·50 to 0·495. Thus, until the number and accuracy of observations have reached a much higher stage, the influence of environment need not be considered.

(3) A noteworthy conclusion reached by biometric workers by actual measurements on man is that the correlation of brothers is not much larger than the correlation of parent and offspring. *A priori*, we

* A German writer has recently given a formula for correcting fraternal correlation for the influence of environment. It differs from the above form, and consists in a factor multiplying r_{12}. He assumes that the high values found for the parental and fraternal correlations in man as compared with those to be expected for *somatic* characters in the Mendelian hypothesis are due to the neglect of the influence of environment by the biometricians. He was probably unaware of the amount of attention which has been given by the biometric school to the determination of environmental correlations and to the comparison of the correlations for characters where environment is likely and unlikely to produce effect, *e.g.* heredity in stature and forearm with heredity in eye-colour and cephalic index. See W. Weinsberg, 'Zeitschrift für Vererbungslehre' 1909, vol. 1.

should expect it to be larger, for brothers have two parents in common, while between father and son comes in the influence of the mother, exerted only on the latter member of the pair. Thus Sir Francis Galton, in his 'Natural Inheritance' (p. 133), makes the fraternal resemblance *twice* as great as the paternal. Pearson*, dealing with three characters in 12 tables of over 1000 each, found the average correlation for parent and child to be 0·46, and for three characters in nine tables the average fraternal correlation to be 0·52. For eye-colour in man† he found the parental correlation 0·495 and the fraternal 0·475, showing a slightly reversed relationship. Both, however, compel us to affirm that the degrees of resemblance between parent and offspring and between brethren are very nearly equal and differ but slightly from 0·5. The values which Mendelian theory leads us to expect are shown in Table IX.

(4) Further conclusions can be drawn now that the measurement of resemblance between pairs of cousins and between uncles or aunts and nephews or nieces has been completed. Judged by a great variety of characters, the cousin relationship has been found to be as close as, if not closer than, the avuncular relationship. This result is, of course, no more remarkable than that between the parental and fraternal resemblances referred to above. However, in view of the publication of a large number of avuncular correlations which have been worked out in the Statistical Laboratory at University College, it seems desirable to show that it is at least consistent with some one or other theory of heredity. From Table IX it will be seen that on the Mendelian theory the relationship between cousins is as close as that between uncle and nephew.

The point is one which is of considerable importance in medical diagnosis. The parents' brothers and sisters have been usually included, and the cousins excluded, in considering the family history. The fact, however, that a man's cousins resemble him as closely as do his uncles and aunts shows that the cousins, usually more numerous, provide at least as good material for an estimate of his tendencies as his parents' brothers and sisters.

The paradox that a man's father's brother's son resembles him, on the average, as closely as his father's brother, although the additional influence of the father's brother's wife has come in, is only a paradox so long as we overlook the fact that somatic and gametic characters are not causally related but only correlated. Almost any determinantal theory of heredity brings out the fact that, on the average, a man resembles his father as closely as he does his brother, and, further, that he is not more like to his

* 'Biometrika,' vol. 2, pp. 378, 387.

† 'Phil. Trans.,' A, 1900, vol. 195, p. 106.

uncle than to his uncle's son. This point is illustrated in the present paper from the investigation of the collateral correlations of a simple Mendelian population mating at random because that determinantal theory is much in vogue to-day. It will be used here to indicate that the facts reached by observation as to the degrees of resemblance between an individual and his ascendants and collaterals, and considered by some to be paradoxical, are curiously enough legitimate developments of Mendelian theory. If they are paradoxes of biometric observations, they are also paradoxes of Mendelian theory, and highly probably of other determinantal hypotheses which may hereafter be developed.

(5) The three first degrees of collateral relationship are worked out in the following paragraphs, viz.:—

(A) The correlation of siblings, *i.e.* of brethren regardless of sex.
(B) The correlation of uncles and aunts with nephews and nieces.*
(C) The correlation of cousins regardless of sex.

The algebra presents no special difficulties beyond laboriousness.

(6) Starting with the population of the form

$$p^2\,(\mathrm{AA})+2pq\,(\mathrm{A}a)+q^2\,(aa),$$

after $16s$† random matings of pairs of individuals of each class, the types of families produced will be those given in the square brackets in Table I. The frequencies of the families will be the factors which multiply the expressions within the brackets. Thus, for example, the mating of the p^2 individuals possessing the protogenic constituent (AA) with the $2pq$ possessing the hybrid (Aa) gives rise to $2p^3q$ families, in each of which $8s$ individuals have the protogenic constituent (AA) and $8s$ the hybrid constituent (Aa).

* The word "siblings" has been reintroduced and largely accepted as a convenient term for brethren of both sexes, but no like terms are in use to denote uncle or aunt and nephew or niece regardless of sex. Prof. Pearson has suggested *eldersib* for uncle or aunt and *sibmag* for nephew or niece as convenient Anglo-Saxon names.

† The number of matings is taken of the form $16s$ in order to prevent fractions occurring later on in the paper. See Table IV.

Table I.

Second parent.	First parent.		
	p^2 (AA).	$2pq$ (Aa).	q^2 (aa).
p^2 (AA)	$p^4\,[16s\,(\mathrm{AA})]$	$2p^3q\,[8s\,(\mathrm{AA}) + 8s\,(\mathrm{A}a)]$	$p^2q^2\,[16s\,(\mathrm{A}a)]$
$2pq$ (Aa)	$2p^3q\,[8s\,(\mathrm{AA}) + 8s\,(\mathrm{A}a)]$	$4p^2q^2\,[4s\,(\mathrm{AA}) + 8s\,(\mathrm{A}a) + 4s\,(aa)]$	$2pq^3\,[8s\,(\mathrm{A}a) + 8s\,(aa)]$
q^2 (aa)	$p^2q^2\,[16s\,(\mathrm{A}a)]$	$2pq^3\,[8s\,(\mathrm{A}a) + 8s\,(aa)]$	$q^4\,[16s\,(aa)]$

(A.) *Correlation between Brothers.*

(7) From Table I we can pick out all the pairs of brothers and arrange them according to the gametic character exhibited by each member of the pair. The cases which can arise, and the number of pairs of brothers in each case are:—

Both brothers (AA)—

$$p^4 \cdot \tfrac{1}{2} \cdot 16s\,(16s-1) + 2p^3q \cdot \tfrac{1}{2} \cdot 8s\,(8s-1)$$
$$+ 2p^3q \cdot \tfrac{1}{2} \cdot 8s\,(8s-1) + 4p^2q^2 \cdot \tfrac{1}{2} \cdot 4s\,(4s-1).$$

Both brothers (Aa)—

$$2p^3q \cdot \tfrac{1}{2} \cdot 8s\,(8s-1) + p^2q^2 \cdot \tfrac{1}{2} \cdot 16s\,(16s-1) + 2p^3q \cdot \tfrac{1}{2} \cdot 8s\,(8s-1)$$
$$+ 4p^2q^2 \cdot \tfrac{1}{2} \cdot 8s\,(8s-1) + 2pq^3 \cdot \tfrac{1}{2} \cdot 8s\,(8s-1) + p^2q^2 \cdot \tfrac{1}{2} \cdot 16s\,(16s-1)$$
$$+ 2pq^3 \cdot \tfrac{1}{2} \cdot 8s\,(8s-1).$$

Both brothers (aa)—

$$4p^2q^2 \cdot \tfrac{1}{2} \cdot 4s\,(4s-1) + 2pq^3 \cdot \tfrac{1}{2} \cdot 8s\,(8s-1) + 2pq^3 \cdot \tfrac{1}{2} \cdot 8s\,(8s-1)$$
$$+ q^4 \cdot \tfrac{1}{2} \cdot 16s\,(16s-1).$$

One brother (AA), other brother (Aa)—

$$2p^3q \cdot 8s \cdot 8s + 2p^3q \cdot 8s \cdot 8s + 4p^2q^2 \cdot 4s \cdot 8s.$$

One brother (AA), other brother (aa)—

$$4p^2q^2 \cdot 4s \cdot 4s.$$

One brother (Aa), other brother (aa)—

$$4p^2q^2 \cdot 8s \cdot 4s + 2pq^3 \cdot 8s \cdot 8s + 2pq^3 \cdot 8s \cdot 8s.$$

From the above expressions a symmetrical table can be constructed, from which to obtain the *gametic* correlation between brothers. This is given in Table II. By arranging the above expressions under the headings "A" and "not A" another table can be formed to give the *somatic* correlation. This is given in Table III. In both tables the factor $16s$, which multiplies every term occurring, has, for brevity, been omitted.

Table II.—Gametic Correlation between Brothers.
(Factor $16s$ omitted throughout.)

Second brother.	First Brother.			Totals.
	(AA.)	(Aa.)	(aa.)	
(AA)	$(16s-1)p^4+(16s-2)p^3q+(4s-1)p^2q^2$	$16sp^3q+8sp^2q^2$	$4sp^2q^2$	$(16s-1)p^2(p+q)^2$
(Aa)	$16sp^3q+8sp^2q^2$	$(16s-2)p^3q+4(12s-1)p^2q^2+(16s-2)pq^3$	$8sp^2q^2+16spq^3$	$2(16s-1)pq(p+q)^2$
(aa)	$4sp^2q^2$	$8sp^2q^2+16spq^3$	$(4s-1)p^2q^2+(16s-2)pq^3+(16s-1)q^4$	$(16s-1)q^2(p+q)^2$
Totals	$(16s-1)p^2(p+q)^2$	$2(16s-1)pq(p+q)^2$	$(16s-1)q^2(p+q)^2$	$(16s-1)(p+q)^4$

Table III.—Somatic Correlation between Brothers.
(Factor $16s$ omitted throughout.)

Second brother.	First brother.		Totals.
	(A.)	(Not A.)	
(A)	$(16s-1)p^4+4(16s-1)p^3q+(68s-5)p^2q^2+(16s-2)pq^3$.	$12sp^2q^2+16spq^3$	$(16s-1)p(p+q)^2(p+2q)$
(Not A)	$12sp^2q^2+16spq^3$	$(4s-1)p^2q^2+(16s-2)pq^3+(16s-1)q^4$	$(16s-1)q^2(p+q)^2$
Totals	$(16s-1)p(p+q)^2(p+2q)$	$(16s-1)q^2(p+q)^2$	$(16s-1)(p+q)^4$

Since the standard deviations of the totals in these tables are the same in both directions, the correlations can at once be found from a knowledge of the means of the columns.

(8) *Gametic Correlation.*—If, in Table II, $\bar{y}_1$, $\bar{y}_2$, $\bar{y}_3$, and $\bar{y}$ are the means of the first, second, and third columns, and of the whole table respectively, each being measured from the centre of the middle row, we find

$$\bar{y}_1 = \frac{(16s-1)p^2+(16s-2)pq-q^2}{(16s-1)(p+q)^2} = \frac{(16s-1)p-q}{(16s-1)(p+q)},$$

$$\bar{y}_2 = \frac{8s(p^2-q^2)}{(16s-1)(p+q)^2} = \frac{8s(p-q)}{(16s-1)(p+q)},$$

$$\bar{y}_3 = \frac{p^2-(16s-2)pq-(16s-1)q^2}{(16s-1)(p+q)^2} = \frac{p-(16s-1)q}{(16s-1)(p+q)},$$

$$\bar{y} = \frac{16s(16s-1)(p+q)^2(p^2-q^2)}{16s(16s-1)(p+q)^4} = \frac{p-q}{p+q}.$$

Hence $$\bar{y}_1-\bar{y}_2 = \frac{8s-1}{16s-1} = \bar{y}_2-\bar{y}_3 = r,$$

from which it follows that the regression is linear and the correlation is $\frac{8s-1}{16s-1}$.

(9) *Somatic Correlation.*—In this case, from Table III, we have, measuring from the "not A" row,

$$\bar{y}_1 = \frac{(16s-1)p^3+4(16s-1)p^2q+(68s-5)pq^2+(16s-2)q^3}{(16s-1)(p+q)^2(p+2q)},$$

$$\bar{y}_2 = \frac{12sp^2+16spq}{(16s-1)(p+q)^2},$$

$$\bar{y} = \frac{p(p+2q)}{(p+q)^2},$$

$$\bar{y}_1-\bar{y}_2 = \frac{(4s-1)p+(16s-2)q}{(16s-1)(p+2q)} = r.$$

The *somatic* correlation therefore depends upon the ratio of p to q, *i.e.* upon the ratio of the number of individuals in the population possessing the dominant character to the number possessing the recedent. For different values of p and q the above value of r can range between $\frac{4s-1}{16s-1}$ and $\frac{1}{2}\cdot\frac{16s-2}{16s-1}$. If $p = q$ its value is $\frac{20s-3}{3(16s-1)}$.*

(10) In considering the value to be given to s in these formulæ in order that they can be compared with statistical results, we must remember that the latter are obtained from families of varying size, from which we take selections of fraternal couples. We must therefore look upon our observations as forming a random sample of all the possible pairs of brethren obtained from an indefinitely large number of matings. That is, we must make s indefinitely large. Then we get the *gametic* correlation to be $\frac{1}{2}$, and the range for the *somatic* correlation from $\frac{1}{4}$ to $\frac{1}{2}$, with the value $\frac{5}{12}$ when $p = q$.

* This particular value of the *somatic* fraternal correlation was reached by Prof. Pearson in his memoir in the 'Phil. Trans.,' A, 1904, vol. 203. In that memoir he dealt with *somatic* characters only, and he assumed the population to be generated from a series of hybridisations and not from a combination of individuals exhibiting the protogenic, allogenic and hybrid constituents in certain proportions. But he was more general in his supposition that the character depended upon n Mendelian couplets, and not on a single one.

(B.) *Correlation between Uncle and Nephew.*

(11) In this case we require not only the various types of families given in Table I, but also the offspring of these families when mated at random. But it will not be sufficient to mate the nine types of families given by Table I with the general population in which the proportions possessing the protogenic, hybrid, and allogenic constituents are p^2(AA), $2pq$(Aa), and q^2(aa), for any particular mating will be of a member of one type of family with a member of the same or another type. An avuncular relationship will arise with the members of both families from which the mating couples are selected. Thus we must discover the offspring which arise from the mating of each type of family in Table I with itself and with each other. This is given in Table IV, in which $4t$ is taken to be the number of matings of each pair. This allows for a possible change of fertility in consecutive generations.

(12) To explain Table IV, consider, for example, the mating of the family of type $4s$(AA)+$8s$(Aa)+$4s$(aa) [Type α] with the family of type $8s$(AA)+$8s$(Aa) [Type β]. Of the $8s$(AA) of Type β:—

- $2s$ will mate with $2s$ of the $4s$(AA) from Type α, giving $4t\{2s(\mathrm{AA})\}$ offspring.
- $4s$ will mate with $4s$ of the $8s$(Aa) from Type α, giving $2t\{4s(\mathrm{AA})\}+2t\{4s(\mathrm{A}a)\}$ offspring.
- $2s$ will mate with $2s$ of the $4s$(aa) from Type α, giving $4t\{2s(\mathrm{A}a)\}$ offspring.

Of the $8s$(Aa) of Type β:—

- $2s$ will mate with $2s$ of the $4s$(AA) from Type α, giving $2t\{2s(\mathrm{AA})\}+2t\{2s(\mathrm{A}a)\}$ offspring.
- $4s$ will mate with $4s$ of the $8s$(Aa) from Type α, giving $t\{4s(\mathrm{AA})\}+2t\{4s(\mathrm{A}a)\}+t\{4s(aa)\}$ offspring.
- $2s$ will mate with $2s$ of the $4s$(aa) from Type α, giving $2t\{2s(\mathrm{A}a)\}+2t\{2s(aa)\}$ offspring.

The complete result will consist of the aggregation of the six combinations written out. Since the frequency of the Type α family is $4p^2q^2$, and of the Type β is $4p^3q$, there will be altogether $16p^5q^3$ such aggregations as the above. The result is represented in the table, in which the families derived through any particular individual exhibiting the constituent (AA), (Aa), or (aa) are written in the same horizontal or vertical line as the constituent itself. The remaining aggregations can be read off in like manner.

(13) From Table IV we can pick out uncle and nephew in pairs according

Table IV.—Showing the Types and Frequencies of the Familie[s]

	p^4 $16s\,(AA)$	$4p^3q$ $8s\,(AA) + 8s\,(Aa)$	$4p^2q^2$ $4s\,(AA) + 8s\,(Aa) + 4s\,(aa)$
$p^4\{16s\,(AA)$	p^8 $4t\,[16s\,(AA)]$	$4p^7q$ $4t\,[8s\,(AA)] + 2t\,[8s\,(AA)] + 2t\,[8s\,(Aa)]$	$4p^6q^2$ $4t\,[4s\,(AA)] + 2t\,[8s\,(AA)] + 2t\,[8s\,(Aa)] + 4t\,[4s\,(Aa)$
$4p^3q$ $\{8s\,(AA) + 8s\,(Aa)$	$4p^7q$ $4t\,[8s\,(AA)]$ $+$ $2t\,[8s\,(AA)] + 2t\,[8s\,(Aa)]$	$16p^6q^2$ $4t\,[4s\,(AA)] + 2t\,[4s\,(AA)] + 2t\,[4s\,(Aa)]$ $+$ $+$ $2t\,[4s\,(AA)] + 2t\,[4s\,(Aa)]$; $t\,[4s\,(AA)] + 2t\,[4s\,(Aa)] + t\,[4s\,(aa)]$	$16p^5q^3$ $4t\,[2s\,(AA)] + 2t\,[4s\,(AA)] + 2t\,[4s\,(Aa)] + 4t\,[2s\,(Aa)$ $+$ $+$ $+$ $2t\,[2s\,(AA)] + 2t\,[2s\,(Aa)]$; $t\,[4s\,(AA)] + 2t\,[4s\,(Aa)] + t\,[4s\,(aa)]$; $2t\,[2s\,(Aa)$ $+ 2t\,[2s\,(aa)]$
$4p^2q^2$ $\{4s\,(AA) + 8s\,(Aa) + 4s\,(aa)$	$4p^6q^2$ $4t\,[4s\,(AA)]$ $+$ $2t\,[8s\,(AA)] + 2t\,[8s\,(Aa)]$ $+$ $4t\,[4s\,(Aa)]$	$16p^5q^3$ $4t\,[2s\,(AA)] + 2t\,[2s\,(AA)] + 2t\,[2s\,(Aa)]$ $+$ $+$ $2t\,[4s\,(AA)] + 2t\,[4s\,(Aa)]$; $t\,[4s\,(AA)] + 2t\,[4s\,(Aa)] + t\,[4s\,(aa)]$ $+$ $+$ $4t\,[2s\,(Aa)]$; $2t\,[2s\,(Aa)] + 2t\,[2s\,(aa)]$	$16p^4q^4$ $4t\,[s\,(AA)] + 2t\,[2s\,(AA)] + 2t\,[2s\,(Aa)] + 4t\,[s\,(Aa)]$ $+$ $+$ $+$ $2t\,[2s\,(AA)] + 2t\,[2s\,(Aa)]$; $t\,[4s\,(AA)] + 2t\,[4s\,(Aa)] + t\,[4s\,(aa)]$; $2t\,[2s\,(Aa)$ $+ 2t\,[2s\,(aa)]$ $+$ $+$ $+$ $4t\,[s\,(Aa)]$; $2t\,[2s\,(Aa)] + 2t\,[2s\,(aa)]$; $4t\,[s\,(aa)]$
$2p^2q^2\{16s\,(Aa)$	$2p^6q^2$ $2t\,[16s\,(AA)] + 2t\,[16s\,(Aa)]$	$8p^5q^3$ $2t\,[8s\,(AA)] + 2t\,[8s\,(Aa)] + t\,[8s\,(AA)] + 2t\,[8s\,(Aa)] + t\,[8s\,(aa)]$	$8p^4q^4$ $2t\,(4s\,(AA)] + 2t\,(4s\,(Aa)] + t\,[8s\,(AA)] + 2t\,[8s\,(Aa)] + t\,[8s\,(aa)] + 2t\,[4s\,(Aa)$ $+ 2t\,[4s\,(aa)]$
$4pq^3$ $\{8s\,(Aa) + 8s\,(aa)$	$4p^5q^3$ $2t\,[8s\,(AA)] + 2t\,[8s\,(Aa)]$ $+$ $4t\,[8s\,(Aa)]$	$16p^4q^4$ $2t\,[4s\,(AA)] + 2t\,[4s\,(Aa)] + t\,[4s\,(AA)] + 2t\,[4s\,(Aa)] + t\,[4s\,(aa)]$ $+$ $+$ $4t\,[4s\,(Aa)]$; $2t\,[4s\,(Aa)] + 2t\,[4s\,(aa)]$	$16p^3q^5$ $2t\,[2s\,(AA)] + 2t\,[2s\,(Aa)] + t\,[4s\,(AA)] + 2t\,[4s\,(Aa)] + t\,[4s\,(aa)] + 2t\,[2s\,(Aa)$ $+ 2t\,[2s\,(aa)]$ $+$ $+$ $+$ $4t\,[2s\,(Aa)]$; $2t\,[4s\,(Aa)] + 2t\,[4s\,(aa)]$; $4t\,[2s\,(aa)]$
$q^4\{16s\,(aa)$	p^4q^4 $4t\,[16s\,(Aa)]$	$4p^3q^5$ $4t\,[8s\,(Aa)] + 2t\,[8s\,(Aa)] + 2t\,[8s\,(aa)]$	$4p^2q^6$ $4t\,[4s\,(Aa)] + 2t\,[8s\,(Aa)] + 2t\,[8s\,(aa)] + 4t\,[4s\,(aa)]$

Families of the Second Generation.

	$2p^2q^2$	$4pq^3$	q^4
$s(aa)$	$16s(\mathrm{A}a)$	$8s(\mathrm{A}a) + 8s(aa)$	$16s(aa)$
$[4s(\mathrm{A}a)]$	$2p^6q^2$ $2t[16s(\mathrm{AA})]$ $+2t[16s(\mathrm{A}a)]$	$4p^5q^3$ $2t[8s(\mathrm{AA})]$ $+2t[8s(\mathrm{A}a)]$ $+$ $4t[8s(\mathrm{A}a)]$	p^4q^4 $4t[16s(\mathrm{A}a)]$
$[2s(\mathrm{A}a)]$ $+$ $[2s(\mathrm{A}a)]$ $[2s(aa)]$	$8p^5q^3$ $2t[8s(\mathrm{AA})]$ $+2t[8s(\mathrm{A}a)]$ $+$ $t[8s(\mathrm{AA})]$ $+2t[8s(\mathrm{A}a)]$ $+\ t[8s(aa)]$	$16p^4q^4$ $2t[4s(\mathrm{AA})]$ $+2t[4s(\mathrm{A}a)]$ $+$ $4t[4s(\mathrm{A}a)]$ $+$ $\quad$ $+$ $t[4s(\mathrm{AA})]$ $+2t[4s(\mathrm{A}a)]$ $+\ t[4s(aa)]$ $\quad$ $2t[4s(\mathrm{A}a)]$ $+2t[4s(aa)]$	$4p^3q^5$ $4t[8s(\mathrm{A}a)]$ $+$ $2t[8s(\mathrm{A}a)]$ $+2t[8s(aa)]$
$[s(\mathrm{A}a)]$ $+$ $[2s(\mathrm{A}a)]$ $[2s(aa)]$ $+$ $[s(aa)]$	$8p^4q^4$ $2t[4s(\mathrm{AA})]$ $+2t[4s(\mathrm{A}a)]$ $+$ $t[8s(\mathrm{AA})]$ $+2t[8s(\mathrm{A}a)]$ $+\ t[8s(aa)]$ $+$ $2t[4s(\mathrm{A}a)]$ $+2t[4s(aa)]$	$16p^3q^5$ $2t[2s(\mathrm{AA})]$ $+2t[2s(\mathrm{A}a)]$ $+$ $4t[2s(\mathrm{A}a)]$ $+$ $\quad$ $+$ $t[4s(\mathrm{AA})]$ $+2t[4s(\mathrm{A}a)]$ $+\ t[4s(aa)]$ $\quad$ $2t[4s(\mathrm{A}a)]$ $+2t[4s(aa)]$ $+$ $\quad$ $+$ $2t[2s(\mathrm{A}a)]$ $+2t[2s(aa)]$ $\quad$ $4t[2s(aa)]$	$4p^2q^6$ $4t[4s(\mathrm{A}a)]$ $+$ $2t[8s(\mathrm{A}a)]$ $+2t[8s(aa)]$ $+$ $4t[4s(aa)]$
$[4s(\mathrm{A}a)]$ $[4s(aa)]$	$4p^4q^4$ $t[16s(\mathrm{AA})]$ $+2t[16s(\mathrm{A}a)]$ $+\ t[16s(aa)]$	$8p^3q^5$ $t[8s(\mathrm{AA})]$ $+2t[8s(\mathrm{A}a)]$ $+$ $2t[8s(\mathrm{A}a)]$ $+\ t[8s(aa)]$ $\quad$ $+2t[8s(aa)]$	$2p^2q^6$ $2t[16s(\mathrm{A}a)]$ $+2t[16s(aa)]$
$[2s(\mathrm{A}a)]$ $[2s(aa)]$ $+$ $[2s(aa)]$	$8p^3q^5$ $t[8s(\mathrm{AA})]$ $+2t[8s(\mathrm{A}a)]$ $+\ t[8s(aa)]$ $+$ $2t[8s(\mathrm{A}a)]$ $+2t[8s(aa)]$	$16p^2q^6$ $t[4s(\mathrm{AA})]$ $+2t[4s(\mathrm{A}a)]$ $+$ $2t[4s(\mathrm{A}a)]$ $+\ t[4s(aa)]$ $\quad$ $+2t[4s(aa)]$ $+$ $\quad$ $+$ $2t[4s(\mathrm{A}a)]$ $+2t[4s(aa)]$ $\quad$ $4t[4s(aa)]$	$4pq^7$ $2t[8s(\mathrm{A}a)]$ $+2t[8s(aa)]$ $+$ $4t[8s(aa)]$
$[4s(aa)]$	$2p^2q^6$ $2t[16s(\mathrm{A}a)]$ $+2t[16s(aa)]$	$4pq^7$ $2t[8s(\mathrm{A}a)]$ $+2t[8s(aa)]$ $+$ $4t[8s(aa)]$	q^8 $4t[16s(aa)]$

to the particular constituent, protogenic, hybrid, or allogenic, each member of the pair possesses. It will be more convenient, however, to make use of the fact that the number of pairs of uncle and nephew will be equal to the number of pairs obtained by taking any one of the children from given parents with any one of the grandchildren, minus the number of pairs of parents and offspring among such pairs. This latter can be obtained more simply than by Table IV. For Table I enables us to pick out parent and offspring in pairs and arrange them according as each member of the pair is (AA), (Aa), or (aa). But we require the number of such pairs in the next generation. Allowing for the change in the fertility from $16s$ to $4t$, it is clear that the number in the second generation will be obtained from the number in the first by writing $4t$ for $16s$ and multiplying by $16s\ (p+q)^4$. From Table I we can at once pick out the following terms for the first generation.

Parent (AA),	offspring (AA)	......	$p^4 . 16s + 2p^3q . 8s$,
„ (AA),	„ (Aa)	......	$2p^3q . 8s + p^2q^2 . 16s$,
„ (AA),	„ (aa)	......	0,
„ (Aa),	„ (AA)	......	$2p^3q . 8s + 4p^2q^2 . 4s$,
„ (Aa),	„ (Aa)	......	$2p^3q . 8s + 4p^2q^2 . 8s + 2pq^3 . 8s$,
„ (Aa),	„ (aa)	......	$4p^2q^2 . 4s + 2pq^3 . 8s$,
„ (aa),	„ (AA)	......	0,
„ (aa),	„ (Aa)	......	$p^2q^2 . 16s + 2pq^3 . 8s$,
„ (aa),	„ (aa)	......	$2pq^3 . 8s + q^4 . 16s$.

In obtaining these expressions, one parent only was considered. From the symmetry of the table, if both parents are to be taken into account, each term must be multiplied by two. Since this factor will occur throughout the work, it can be omitted.

Collecting the above terms, and applying the modification necessary to transform the first generation into the second, we have, for this latter generation, the frequencies :—

Parent (AA),	offspring (AA)	......	$64st\,p^3\,(p+q)^5$,
„ (AA),	„ (Aa)	......	$64st\,p^2q\,(p+q)^5$,
„ (AA),	„ (aa)	......	0,
„ (Aa),	„ (AA)	......	$64st\,p^2q\,(p+q)^5$,
„ (Aa),	„ (Aa)	......	$64st\,pq\,(p+q)^6$,
„ (Aa),	„ (aa)	......	$64st\,pq^2\,(p+q)^5$,
„ (aa),	„ (AA)	......	0,
„ (aa),	„ (Aa)	......	$64st\,pq^2\,(p+q)^5$,
„ (aa),	„ (aa)	......	$64st\,q^3\,(p+q)^5$.

From Table IV we have now to pick out and arrange the various pairs

which can be obtained by taking any one in the first generation with any one of the same stock in the second generation (*i.e.* both sons and nephews).

To economise space, the details of the terms are given in the case of three only of the nine pairs. The other six can be written out in the same manner, but the results alone are stated. The three pairs given in detail are:—

Member of the first generation (AA), member of the second generation (AA)—

$$\begin{aligned}
&p^8 . 16s . 4t . 16s + 4p^7q . 16s . (4t . 8s + 2t . 8s) \\
&+ 4p^6q^2 . 16s (4t . 4s + 2t . 8s) + 2p^6q^2 . 16s . 2t . 16s \\
&+ 4p^5q^3 . 16s . 2t . 8s + 4p^7q . 8s (4t . 8s + 2t . 8s) \\
&+ 16p^6q^2 . 8s (4t . 4s + 2t . 4s + 2t . 4s + t . 4s) \\
&+ 16p^5q^3 . 8s (4t . 2s + 2t . 4s + 2t . 2s + t . 4s) \\
&+ 8p^5q^3 . 8s (2t . 8s + t . 8s) + 16p^4q^4 . 8s (2t . 4s + t . 4s) \\
&+ 4p^6q^2 . 4s (4t . 4s + 2t . 8s) + 16p^5q^3 . 4s (4t . 2s + 2t . 4s + 2t . 2s + t . 4s) \\
&+ 16p^4q^4 . 4s (4t . s + 2t . 2s + 2t . 2s + t . 4s) \\
&+ 8p^4q^4 . 4s (2t . 4s + t . 8s) + 16p^3q^5 . 4s (2t . 2s + t . 4s).
\end{aligned}$$

When these terms are collected, and simplification performed, the whole expression reduces to the simple form

$$512s^2tp^3 (p+q)^4 (2p+q).$$

Member of first generation (AA), member of second generation (A*a*)—

$$\begin{aligned}
&4p^7q . 16s . 2t . 8s + 4p^6q^2 . 16s (2t . 8s + 4t . 4s) + 2p^6q^2 . 16s . 2t . 16s \\
&+ 4p^5q^3 . 16s (2t . 8s + 4t . 8s) + p^4q^4 . 16s . 4t . 16s \\
&+ 4p^7q . 8s . 2t . 8s + 16p^6q^2 . 8s (2t . 4s + 2t . 4s + 2t . 4s) \\
&+ 16p^5q^3 . 8s (2t . 2s + 2t . 4s + 2t . 4s + 4t . 2s + 2t . 2s) \\
&+ 8p^5q^3 . 8s (2t . 8s + 2t . 8s) + 16p^4q^4 . 8s (2t . 4s + 2t . 4s + 4t . 4s + 2t . 4s) \\
&+ 4p^3q^5 . 8s (4t . 8s + 2t . 8s) + 4p^6q^2 . 4s (2t . 8s + 4t . 4s) \\
&+ 16p^5q^3 . 4s (2t . 4s + 4t . 2s + 2t . 2s + 2t . 4s + 2t . 2s) \\
&+ 16p^4q^4 . 4s (2t . 2s + 4t . s + 2t . 2s + 2t . 4s + 2t . 2s + 4t . s + 2t . 2s) \\
&+ 8p^4q^4 . 4s (2t . 4s + 2t . 8s + 2t . 4s) \\
&+ 16p^3q^5 . 4s (2t . 2s + 2t . 4s + 2t . 2s + 4t . 2s + 2t . 4s) \\
&+ 4p^2q^6 . 4s (4t . 4s + 2t . 8s).
\end{aligned}$$

This, when simplified, becomes

$$512s^2tp^2q (p+q)^4 (3p+q).$$

Member of first generation (AA), member of second generation (aa)—

$$16p^6q^2 \,.\, 8s \,.\, t \,.\, 4s + 16p^5q^3 \,.\, 8s\,(t \,.\, 4s + 2t \,.\, 2s) + 8p^5q^3 \,.\, 8s \,.\, t \,.\, 8s$$
$$+ 16p^4q^4 \,.\, 8s\,(t \,.\, 4s + 2t \,.\, 4s) + 4p^3q^5 \,.\, 8s \,.\, 2t \,.\, 8s$$
$$+ 16p^5q^3 \,.\, 4s\,(t \,.\, 4s + 2t \,.\, 2s) + 16p^4q^4 \,.\, 4s\,(t \,.\, 4s + 2t \,.\, 2s + 2t \,.\, 2s + 4t \,.\, s)$$
$$+ 8p^4q^4 \,.\, 4s\,(t \,.\, 8s + 2t \,.\, 4s) + 16p^3q^5 \,.\, 4s\,(t \,.\, 4s + 2t \,.\, 2s + 2t \,.\, 4s + 4t \,.\, 2s)$$
$$+ 4p^2q^6 \,.\, 4s\,(2t \,.\, 8s + 4t \,.\, 4s).$$

This reduces to $512s^2t\,p^2q^2\,(p+q)^4$.

The frequencies of the other pairs are (the member of the first generation in each case being placed first)

$(\mathrm{A}a)$ with (AA)……		$512s^2t\,p^2q\,(p+q)^4\,(3p+q)$,
$(\mathrm{A}a)$ „	$(\mathrm{A}a)$……	$512s^2t\,pq\,(p+q)^4\,(p^2+6pq+q^2)$,
$(\mathrm{A}a)$ „	(aa)……	$512s^2t\,pq^2\,(p+q)^4\,(p+3q)$,
(aa) „	(AA)……	$512s^2t\,p^2q^2\,(p+q)^4$,
(aa) „	$(\mathrm{A}a)$……	$512s^2t\,pq^2\,(p+q)^4\,(p+3q)$,
(aa) „	(aa)……	$512s^2t\,q^3\,(p+q)^4\,(p+2q)$.

Subtracting from these expressions those found for the corresponding combinations in the case of parent and offspring of the second generation given above, we get the following frequencies for combinations of uncle and nephew :—

Uncle (AA),	nephew (AA)…	$64st\,p^3\,(p+q)^4\,[(16s-1)\,p+(8s-1)\,q]$,
„ (AA),	„ $(\mathrm{A}a)$…	$64st\,pq\,(p+q)^4\,[(24s-1)\,p^2+(8s-1)\,pq]$,
„ (AA),	„ (aa)…	$512s^2t\,p^2q^2\,(p+q)^4$.
„ $(\mathrm{A}a)$,	„ (AA)…	$64st\,pq\,(p+q)^4\,[(24s-1)p^2+(8s-1)\,pq]$,
„ $(\mathrm{A}a)$,	„ $(\mathrm{A}a)$…	$64st\,pq\,(p+q)^4\,[(8s-1)\,p^2+(48s-2)\,pq+(8s-1)\,q^2]$,
„ $(\mathrm{A}a)$,	„ (aa)…	$64st\,pq^2\,(p+q)^4\,[(8s-1)\,p+(24s-1)\,q]$,
„ (aa),	„ (AA)…	$512s^2t\,p^2q^2\,(p+q)^4$,
„ (aa),	„ $(\mathrm{A}a)$…	$64st\,pq^2\,(p+q)^4\,[(8s-1)\,p+(24s-1)\,q]$,
„ (aa),	„ (aa)…	$64st\,q^3\,(p+q)^4\,[(8s-1)\,p+(16s-1)\,q]$.

Correlation tables can now be formed from which to derive the gametic and the somatic relationships between uncle and nephew. Table V gives the *gametic* relationship; Table VI the *somatic*. In both of these tables the factor $64\,st\,(p+q)^4$, which multiplies every cell, has been omitted.

Table V.—Gametic Correlation between Uncle and Nephew.

(Factor $64\,st\,(p+q)^4$ omitted throughout.)

Nephew.	Uncle. (AA.)	Uncle. (Aa.)	Uncle. (aa.)	Totals.
(AA)	$(16s-1)p^4+(8s-1)p^3q$	$(24s-1)p^3q+(8s-1)p^2q^2$	$8sp^2q^2$	$(16s-1)p^2(p+q)^2$
(Aa)	$(24s-1)p^3q+(8s-1)p^2q^2$	$(8s-1)p^3q+(48s-2)p^2q^2+(8s-1)pq^3$	$(8s-1)p^2q^2+(24s-1)pq^3$	$2(16s-1)pq(p+q)^2$
(aa)	$8sp^2q^2$	$(8-s1)p^2q^2+(24s-1)pq^3$	$(8s-1)pq^3+(16s-1)q^4$	$(16s-1)q^2(p+q)^2$
Totals	$(16s-1)p^2(p+q)^2$	$2(16s-1)pq(p+q)^2$	$(16s-1)q^2(p+q)^2$	$(16s-1)(p+q)^4$

Table VI.—Somatic Correlation between Uncle and Nephew.

(Factor $64st\,(p+q)^4$ omitted throughout.)

Nephew.	Uncle. (A.)	Uncle. (Not A.)	Totals.
(A)	$(16s-1)p^4+4(16s-1)p^3q+4(16s-1)p^2q^2+(8s-1)pq^3$	$(16s-1)p^2q^2+(24s-1)pq^3$	$(16s-1)p(p+q)^2(p+2q)$
(Not A)	$(16s-1)p^2q^2+(24s-1)pq^3$	$(8s-1)pq^3+(16s-1)q^4$	$(16s-1)q^2(p+q)^2$
Totals	$(16s-1)p(p+q)^2(p+2q)$	$(16s-1)q^2(p+q)^2$	$(16s-1)(p+q)^4$

(14) *Gametic Correlation.*—From Table V we find, measuring from the centre of the middle row—

$$\bar{y}_1 = \frac{(16s-1)p^2+(8s-1)pq-8sq^2}{(16s-1)(p+q)^2} \qquad \bar{y}_3 = \frac{8sp^2-(8s-1)pq-(16s-1)q^2}{(16s-1)(p+q)^2},$$

$$\bar{y}_2 = \frac{(24s-1)(p^2-q^2)}{2(16s-1)(p+q)^2} \qquad \bar{y} = \frac{p^2-q^2}{(p+q)^2} = \frac{p-q}{p+q}.$$

Hence
$$\bar{y}_1-\bar{y}_2 = \frac{8s-1}{16s-1}\cdot\frac{1}{2} = \bar{y}_2-\bar{y}_3 = r.$$

Therefore the regression is linear and the correlation $\frac{8s-1}{16s-1}\cdot\frac{1}{2}$. As before, we must take a random sample from the families obtained by making s indefinitely large. The correlation then becomes $\frac{1}{4}$.

(15) *Somatic Correlation.*—Table VI gives, measuring from the "not A" row—

$$\bar{y} = \frac{p(p+2q)}{(p+q)^2}$$

and
$$\bar{y}_1 - \bar{y}_2 = \frac{8s-1}{16s-1} \cdot \frac{q}{p+2q} = r.$$

Again the correlation depends upon the relative values of p and q. The limits between which r can lie for different values of p and q are 0 and $\frac{8s-1}{16s-1} \cdot \frac{1}{2}$. If $p = q$, its value is $\frac{8s-1}{16s-1} \cdot \frac{1}{3}$. Putting s infinite, the range for r is from 0 to $\frac{1}{4}$, with the value $\frac{1}{6}$ when $p = q$.

(C.) *Correlation between First Cousins.*

(16) From Table IV we can pick out every pair of first cousins, and arrange them in groups according as each member of the pair exhibits the constituent (AA), (A*a*) or (*aa*). But, again, it is more convenient to obtain these groups indirectly. For the number of pairs of cousins in any group will be equal to the number of pairs which can be taken from all children having the same two grandparents, minus the number of pairs of brothers among such children. Since the population is stable during succeeding generations, the latter can be obtained at once from the expressions given in (7) by writing $4t$ for $16s$ in that table and multiplying by the factor $16s(p+q)^4$. We therefore have the following expressions for the number of pairs of brothers among all grandchildren :—

First brother.	Second brother.	
(AA)	(AA)......	$32st(p+q)^4[(4t-1)p^4+(4t-2)p^3q+(t-1)p^2q^2]$,
(AA)	(A*a*)	$64st(p+q)^4[4tp^3q+2tp^2q^2]$,
(AA)	(*aa*)	$64st(p+q)^4 tp^2q^2$,
(A*a*)	(A*a*)	$32st(p+q)^4[(4t-2)p^3q+4(3t-1)p^2q^2+(4t-2)pq^3]$,
(A*a*)	(*aa*)	$64st(p+q)^4[2tp^2q^2+4tpq^3]$,
(*aa*)	(*aa*)	$32st(p+q)^4[(t-1)p^2q^2+(4t-2)pq^3+(4t-1)q^4]$.

The number of pairs of all possible grandchildren (*i.e.* siblings, together with cousins) can be easily obtained from inspection of Table IV. From symmetry, only six combinations are now required. Three of these are given in detail, the final expressions only of the other three being written down. Throughout the detailed expressions k is written for the product *s.t.*

First grandchild (AA), second grandchild (AA)—

$$p^8 \cdot \tfrac{1}{2} \cdot 64k(64k-1) + 4p^7q \cdot \tfrac{1}{2} \cdot 48k(48k-1) + 4p^6q^2 \cdot \tfrac{1}{2} \cdot 32k(32k-1)$$
$$+2p^6q^2 \cdot \tfrac{1}{2} \cdot 32k(32k-1) + 4p^5q^3 \cdot \tfrac{1}{2} \cdot 16k(16k-1) + 4p^7q \cdot \tfrac{1}{2} \cdot 48k(48k-1)$$
$$+16p^6q^2 \cdot \tfrac{1}{2} \cdot 36k(36k-1) + 16p^5q^3 \cdot \tfrac{1}{2} \cdot 24k(24k-1) + 8p^5q^3 \cdot \tfrac{1}{2} \cdot 24k(24k-1)$$
$$+16p^4q^4 \cdot \tfrac{1}{2} \cdot 12k(12k-1) + 4p^6q^2 \cdot \tfrac{1}{2} \cdot 32k(32k-1) + 16p^5q^3 \cdot \tfrac{1}{2} \cdot 24k(24k-1)$$
$$+16p^4q^4 \cdot \tfrac{1}{2} \cdot 16k(16k-1) + 8p^4q^4 \cdot \tfrac{1}{2} \cdot 16k(16k-1) + 16p^3q^5 \cdot \tfrac{1}{2} \cdot 8k(8k-1)$$
$$+2p^6q^2 \cdot \tfrac{1}{2} \cdot 32k(32k-1) + 8p^5q^3 \cdot \tfrac{1}{2} \cdot 24k(24k-1) + 8p^4q^4 \cdot \tfrac{1}{2} \cdot 16k(16k-1)$$
$$+4p^4q^4 \cdot \tfrac{1}{2} \cdot 16k(16k-1) + 8p^3q^5 \cdot \tfrac{1}{2} \cdot 8k(8k-1) + 4p^5q^3 \cdot \tfrac{1}{2} \cdot 16k(16k-1)$$
$$+16p^4q^4 \cdot \tfrac{1}{2} \cdot 12k(12k-1) + 16p^3q^5 \cdot \tfrac{1}{2} \cdot 8k(8k-1) + 8p^3q^5 \cdot \tfrac{1}{2} \cdot 8k(8k-1)$$
$$+16p^2q^6 \cdot \tfrac{1}{2} \cdot 4k(4k-1).$$

This reduces to

$$32st\,p^2(p+q)^4[(64st-1)p^2 + (32st-2)pq + (4st-1)q^2].$$

First grandchild (AA), second grandchild (Aa)—

$$4p^7q \cdot 48k \cdot 16k + 4p^6q^2 \cdot 32k \cdot 32k + 2p^6q^2 \cdot 32k \cdot 32k$$
$$+4p^5q^3 \cdot 16k \cdot 48k + 4p^7q \cdot 48k \cdot 16k + 16p^6q^2 \cdot 36k \cdot 24k$$
$$+16p^5q^3 \cdot 24k \cdot 32k + 8p^5q^3 \cdot 24k \cdot 32k + 16p^4q^4 \cdot 12k \cdot 40k$$
$$+4p^6q^2 \cdot 32k \cdot 32k + 16p^5q^3 \cdot 24k \cdot 32k + 16p^4q^4 \cdot 16k \cdot 32k$$
$$+8p^4q^4 \cdot 16k \cdot 32k + 16p^3q^5 \cdot 8k \cdot 32k + 2p^6q^2 \cdot 32k \cdot 32k$$
$$+8p^5q^3 \cdot 24k \cdot 32k + 8p^4q^4 \cdot 16k \cdot 32k + 4p^4q^4 \cdot 16k \cdot 32k$$
$$+8p^3q^5 \cdot 8k \cdot 32k + 4p^5q^3 \cdot 16k \cdot 48k + 16p^4q^4 \cdot 12k \cdot 40k$$
$$+16p^3q^5 \cdot 8k \cdot 32k + 8p^3q^5 \cdot 8k \cdot 32k + 16p^2q^6 \cdot 4k \cdot 24k.$$

This becomes $\qquad 512s^2t^2p^2q(p+q)^4(12p+3q).$

First grandchild (AA), second grandchild (aa)—

$$16p^6q^2 \cdot 36k \cdot 4k + 16p^5q^3 \cdot 24k \cdot 8k + 8p^5q^3 \cdot 24k \cdot 8k$$
$$+16p^4q^4 \cdot 12k \cdot 12k + 16p^5q^3 \cdot 24k \cdot 8k$$
$$+16p^4q^4 \cdot 16k \cdot 16k + 8p^4q^4 \cdot 16k \cdot 16k + 16p^3q^5 \cdot 8k \cdot 24k$$
$$+8p^5q^3 \cdot 24k \cdot 8k + 8p^4q^4 \cdot 16k \cdot 16k + 4p^4q^4 \cdot 16k \cdot 16k$$
$$+8p^3q^5 \cdot 8k \cdot 24k + 16p^4q^4 \cdot 12k \cdot 12k + 16p^3q^5 \cdot 8k \cdot 24k$$
$$+8p^3q^5 \cdot 8k \cdot 24k + 16p^2q^6 \cdot 4k \cdot 36k.$$

This becomes $\qquad 2304s^2t^2p^2q^2(p+q)^4.$

The other combinations reduce to:—

First grandchild (Aa), second grandchild (Aa)—

$$64st\,pq(p+q)^4[(16st-1)p^2 + (104st-2)pq + (16st-1)q^2].$$

First grandchild (Aa), second grandchild (aa)—

$$512 s^2 t^2 pq^2 (p+q)^4 (3p+12q).$$

First grandchild (aa), second grandchild (aa)—

$$32 st\, q^2 (p+q)^4 [(4st-1) p^2 + (32st-2) pq + (64st-1) q^2].$$

To obtain the frequencies of the various pairs of cousins, we have to subtract from the above six expressions the corresponding expressions for pairs of brothers. We then get the following frequencies:—

Both cousins (AA)—$32\, st^2 p^2 (p+q)^4 [64s-4) p^2 + (32s-4) pq + (4s-1) q^2]$.

One cousin (AA), other (Aa)... $128 st^2 p^2 q (p+q)^4 [(48s-2) p + (12s-1) q]$.

" (AA), " (aa) ... $64 st^2 p^2 q^2 (p+q)^4 (36s-1)$.

Both cousins (Aa)—

$$128 st^2 pq (p+q)^4 [(8s-1) p^2 + (52s-3) pq + (8s-1) q^2].$$

One cousin (Aa), other (aa)—

$$128 st^2 pq^2 (p+q)^4 [(12s-1) p + (48s-2) q].$$

Both cousins (aa)—

$$32 st^2 q^2 (p+q)^4 [(4s-1) p^2 + (32s-4) pq + (64s-4) q^2].$$

The correlations tables for cousins can now be formed. Table VII gives the arrangement for the *gametic* relationship, Table VIII for the *somatic*. In both cases the factor $64\, st^2 (p+q)^4$ has been omitted. The tables must, of course, be made symmetrical.

Table VII.—Gametic Correlation between Cousins.
(Factor $64\, st^2 (p+q)^4$ omitted.)

Second cousin.	First cousin.			Totals.
	(AA).	(Aa).	(aa).	
(AA)	$(64s-4) p^4 + (32s-4) p^3 q + (4s-1) p^2 q^2$	$(96s-4) p^3 q + (24s-2) p^2 q^2$	$(36s-1) p^2 q^2$	$4(16s-1) p^2 (p+q)^2$
(Aa)	$(96s-4) p^3 q + (24s-2) p^2 q^2$	$(32s-4) p^3 q + (208s-12) p^2 q^2 + (32s-4) pq^3$	$(24s-2) p^2 q^2 + (96s-4) pq^3$	$8(16s-1) pq (p+q)^2$
(aa)	$(36s-1) p^2 q^2$	$(24s-2) p^2 q^2 + (96s-4) pq^3$	$(4s-1) p^2 q^2 + (32s-4) pq^3 + (64s-4) q^4$	$4(16s-1) q^2 (p+q)^2$
Totals	$4(16s-1) p^2 (p+q)^2$	$8(16s-1) pq (p+q)^2$	$4(16s-1) q^2 (p+q)^2$	$4(16s-1)(p+q)^4$

Table VIII.—Somatic Correlation between Cousins.
(Factor $64st^2(p+q)^4$ omitted.)

Second cousin.	First cousin.		Totals.
	(A).	(Not A).	
(A)	$4(16s-1)p^4+16(16s-1)p^3q$ $+(260s-17)p^2q^2+4(8s-1)pq^3$	$4(24s-1)pq^3+3(20s-1)p^2q^2$	$4(16s-1)(p+q)^2p(p+2q)$
(Not A)	$4(24s-1)pq^3+3(20s-1)p^2q^2$	$4(16s-1)q^4+4(8s-1)pq^3$ $+(4s-1)p^2q^2$	$4(16s-1)q^2(p+q)^2$
Totals	$4(16s-1)(p+q)^2p(p+2q)$	$4(16s-1)q^2(p+q)^2$	$4(16s-1)(p+q)^4$

(17) *Gametic Correlation.*—From Table VII we find, after simplification—

$$\bar{y}_1 = \frac{(16s-1)p-8sq}{(16s-1)(p+q)} \qquad \bar{y}_3 = \frac{8sp-(16s-1)q}{(16s-1)(p+q)}$$

$$\bar{y}_2 = \frac{(24s-1)(p-q)}{2(16s-1)(p+q)} \qquad \bar{y} = \frac{p-q}{p+q}.$$

From these, $\bar{y}_1-\bar{y}_2 = \dfrac{8s-1}{2(16s-1)} = \bar{y}_2-\bar{y}_3 = r$. Hence the regression again is linear, and the correlation $\dfrac{8s-1}{16s-1}\cdot\dfrac{1}{2}$. When s is indefinitely large this becomes $\frac{1}{4}$.

(18) *Somatic Correlation.*—In this case, after reduction, we find—

$$\bar{y} = \frac{p(p+2q)}{(p+q)^2} \quad \text{and} \quad \bar{y}_1-\bar{y}_2 = \frac{(4s-1)p+4(8s-1)q}{4(16s-1)(p+2q)} = r.$$

Hence in the case of cousins also the *somatic* correlation depends upon the ratio of p to q. The range of r for different values of p and q extends from $\dfrac{4s-1}{4(16s-1)}$ to $\dfrac{8s-1}{2(16s-1)}$. If $p=q$ its value is $\dfrac{36s-5}{12(16s-1)}$. When s is indefinitely large, the range is from $\frac{1}{16}$ to $\frac{1}{4}$, with the value $\frac{3}{16}$ when $p=q$.

(19) In Table IX, all the correlations which have been worked out from the Mendelian hypothesis of "unit characters" are collected together. The values of the parental and grandparental correlations are from Prof. Pearson's paper.* The rest have been obtained in the present paper.

* "On the Ancestral Correlations of a Mendelian Population," 'Roy. Soc. Proc.,' B, 1909, vol. 81.

Table IX.—List of *Mendelian* Correlations between an Individual and his Relatives.

Relative.	Gametic correlation.	Somatic correlation.		
		General.	Range.	$p = q$.
Parent	$\frac{1}{2}$	$\frac{q}{p+2q}$	$0-\frac{1}{2}$	$\frac{1}{3}$
Grandparent............	$\frac{1}{4}$	$\frac{q}{p+2q}\cdot\frac{1}{2}$	$0-\frac{1}{4}$	$\frac{1}{6}$
Brother or sister	$\frac{1}{2}$	$\frac{p+4q}{p+2q}\cdot\frac{1}{4}$	$\frac{1}{4}-\frac{1}{2}$	$\frac{5}{12}$
Uncle or aunt	$\frac{1}{4}$	$\frac{q}{p+2q}\cdot\frac{1}{2}$	$0-\frac{1}{4}$	$\frac{1}{6}$
Cousin	$\frac{1}{4}$	$\frac{p+8q}{p+2q}\cdot\frac{1}{16}$	$\frac{1}{16}-\frac{1}{4}$	$\frac{3}{16}$

From this table we notice that, on the Mendelian hypothesis, the parental and sibling gametic correlations are equal, while the grandparental, avuncular, and cousin gametic correlations are also equal and are just one-half of the former. In Table X the ancestral and collateral correlations in man and certain animals founded on biometric research, together with the corresponding *gametic* correlations found above on the Mendelian assumption of "unit-characters," are collected.

(20) The following general conclusions can be drawn from the correlations for *somatic* characters given in Table IX.

(i) If $p > 8q$ the cousin correlation is greater than the parental. This seems remarkable, but it must be borne in mind that the condition is derived from the Mendelian idea of "unit-characters," and no prediction can be made as to when the condition is fulfilled. The only cousin correlations worked out for the biometric school are those by Miss Elderton. No correlation for a single character in cousins was found to exceed the parental one. In eye-colour alone did the former approach the latter. The parental correlation in this case was 0·495, while the cousin correlation had the values 0·44, 0·48, and 0·38 for male and male, male and female, and female and female respectively, the mean value being 0·434.

(ii) If q is small, *i.e.* if the recedent constituent is rare, as in the case of albinism in man, the correlations founded on Mendelism have low values, and in certain cases approach zero. For pathological characters the figures found by Miss Elderton were certainly much smaller than for other characters in

Table X.—Mean Ancestral and Collateral Correlations in Man and Animals.*

—	Parent.	Grand-parent.	Sibling.	Uncle.	Cousin.
Man	0·470	0·317	0·521	0·265	0·267
Horse	0·522	0·296			
Basset hound	0·526	0·220	0·508		
Greyhound	0·532	0·332	0·559		
Shorthorn	0·444	0·200	0·530		
Mean of biometric results	0·498	0·273	0·529	0·265	0·267
Gametic correlation on Mendelian hypothesis.	0·500	0·250	0·500	0·250	0·250

cousins, but this was ascribed to the incompleteness of the records. No general tendency in the direction of lower correlations for certain characters has yet been noticed in biometric investigations.

(iii) The correlation between siblings is always greater than that between parent and offspring. This is in accordance with *a priori* expectation (see para. 3 above) and agrees with statistical results.

(iv) The grandparental correlation is always the same as the avuncular. This also agrees fairly well with statistical conclusions.

In his paper of last year Prof. Pearson drew attention to the fact that the

* Each biometric correlation given in the table is the mean of a number of values and is compiled from the following sources :—

(1) Karl Pearson and Alice Lee, "On the Laws of Inheritance in Man," Parts I and II, 'Biometrika,' vols. 2 and 3.
(2) Karl Pearson, "On Inheritance of the Mental and Moral Characters in Man," *ibid.*, vol. 3.
(3) Amy Barrington, Alice Lee and Karl Pearson, "On Inheritance of Coat Colour in Greyhounds," *ibid.*, vol. 3.
(4) Amy Barrington and Karl Pearson, "On Inheritance of Coat Colour in Cattle," *ibid.*, vol. 4.
(5) Ethel M. Elderton, "On the Measure of the Resemblance of First Cousins," 'Eugenics Laboratory Memoirs,' IV, 1907.

The characters correlated for man include stature, span, forearm and eye-colour. The sibling correlations include also hair-colour, together with those of no less than 16 characters obtained from school records. The mean fraternal correlation based on this homogeneous material was 0·519. The cousin correlations were deduced from eye-colour, hair-colour, health, ability, etc. Among the animals, coat-colour was the character correlated throughout.

values of the ancestral *gametic* correlations in a Mendelian population obtained from theoretical considerations were in close accordance with those determined for the *somatic* characters in biometric researches, while the *somatic* correlation on the Mendelian hypothesis appeared to be too low, if the principle of absolute dominance was maintained. The results of the present paper for the sibling, avuncular and cousin correlations agree equally well with the statement made for ancestral correlations. The general *somatic* correlation for cousins, viz., $\frac{1}{16}\frac{p+8q}{p+2q}$, is always greater than the general *somatic* grandparental and avuncular correlations. The conclusion of Miss Elderton that "cousins must be classed as equally important with uncles and aunts, and they may eventually turn out to be as important as grandparents," paradoxical as it appears, is supported by the theory of Mendelism as well as by biometric experience. Without making any dogmatic assertion, it seems safe to conclude, both from theory and practice, that the cousin ranks in no way behind aunt or uncle and grandparent in family resemblance. The importance of this deduction in medical diagnosis has already been indicated.

In conclusion I have to thank Prof. Pearson for considerable advice while the work in connection with this paper has been in progress.

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